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Colonization of dry habitats by the Song Thrush *Turdus philomelos*: is the type of nest material an important constraint?

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Introduction

Being better adapted to nesting high in trees (when there is no bush layer), to feeding in drier places and more frequently in open areas (Siivonen 1939, Glutz & Bauer 1988, Tomialojć & Lontkowski, in prep.), the Song Thrush *Turdus philomelos* theoretically should cope better with life in dry, urban or Mediterranean habitats than the Blackbird *T. merula*. In fact, the opposite is the case, which constitutes an interesting ecological problem. It may be speculated that the reason may be either that some other constraint on its ecology outweighs the factors favourable to the Song Thrush, mentioned above, or that the Blackbird started to colonize these areas so much earlier that it has managed more thoroughly than the Song Thrush to adapt in other important (but less obvious) ways.

Historical data available so far do not support the second suggestion (Cramp, 1988, Glutz & Bauer 1988). Another suggestion is that the Song Thrush is out-competed by the more adaptable Blackbird (Dyrce 1969); but this seems an unlikely explanation of the problem under consideration, since in rural and urban British and Czechoslovakian habitats both of them, not just the Blackbird, maintain densities much higher than elsewhere (Davies & Snow 1965, Cramp 1988, Stastny *et al.* 1987). This last point will be reconsidered in detail elsewhere (Tomialojć, in prep).

In geographical terms the question is, why the Song Thrush has a very restricted breeding distribution in the Mediterranean region (and in the Eurasian forest-steppe transitional zone). These areas remain outside its main breeding range, though they are regularly visited on migration or in the winter. Isolated breeding areas occur only in higher (more humid?) parts of the Spanish Cordillera Central, Pyrenees, Mont Ventoux, Appennines, Anatolian mountains and Caucasus (Glutz & Bauer 1988, Blondel 1990). This is the more surprising since the apparently more humidity-dependent Blackbird maintains dense breeding populations in the southern part of the western Palearctic.

I hypothesize here that in both types of habitats, urban and Mediterranean, the Song Thrush has a problem with the construction of its peculiar nest. Under dry climatic conditions it probably cannot plaster the inner parts of its nest for a whole complex of reasons: the process of wood rotting seems to be inhibited or prevented in a dry climate, soft-timber trees are rare, old trees become scarce under fire-management regimes, and finally, wood pulp even if present may be too dry for nest plastering. The last obstacle may apply also to the use of clay, mud or dung.

Material and results

One of the noteworthy differences between European Song Thrush populations lies in the kind of nest material that they use. As has been described by Siivonen (1939), Bocheński (1968) and Glutz & Bauer (1988), the nest consists of two or three layers. In contrast to the analysis made by Siivonen, who concentrated on the variability in the outer-layer structure, here we focus attention on the inner-layer materials, as they are very specific in the Song Thrush in comparison with other thrushes (Bocheński 1968). The inner layer of a Song Thrush nest may be made in three different ways:

type 1: exclusively of wood pulp, which directly adjoins the outer layer built of mosses, lichens, dry grasses, leaves or twigs;

type 2: similar to above, but with an additional (median) layer of mud or clay under the wood pulp;

type 3: no wood pulp at all, the inner layer consisting mostly or entirely of earth or dung.

These three types show interesting geographical and ecological patterns of distribution.

Our own data were collected in the Białowieża National Park during studies of the breeding ecology of the Song Thrush and Blackbird populations inhabiting an undisturbed primeval forest (Tomialojć &

TABLE 1
Percentage share of the various types of Song Thrush nests in samples from different parts of central and northern Europe

	<i>n</i>	Type 1	Type 2	Type 3
Forests of Finland (Siivonen 1939)	63?	all/most	?	0
Forests of Leningrad Province (Malchevskiy & Pukinskiy 1983)	195	most	a few	0
Bialowieża primeval forests (this study)	166	94.6	5.4	0
Forests and woods of southern Poland (Bocheński 1968, and <i>in litt.</i>)	111	63	30	6
Secondary and natural habitats in Czechoslovakia (Pikula 1970)	121	17.1	22.0	57.8

Note. Differences between the Bialowieża and Czechoslovakian samples are highly statistically significant ($P < 0.001$, χ^2 test).

Lontkowski, in prep.). Other data were extracted from Z. Bocheński's collection stored in the Department of Systematic Zoology and Evolution of Animals (Cracow), and from the Polish nest-record scheme run by T. Wesolowski, Wrocław. These data (Table 1) show that there is a clear decrease in the proportion of type 1 nests as one proceeds from primeval forest habitats to anthropogenic habitats. This is paralleled to some extent by a geographical trend; thus in the forests of Finland type 1 occurs almost exclusively (Siivonen 1939), in central Europe the situation is diverse (see below), while in Great Britain types 2 or 3 seem to prevail, especially among the Hebridean population (Witherby *et al.* 1940).

Table 1 requires some comments. In the Bialowieża National Park the proportion of type 2 nests may depend on habitat. They constitute 7.2% of the sample from river-side ash-alder forest ($n = 55$), 3.9% from oak-hornbeam or hard-wood forest ($n = 103$), and 6.6% in mixed coniferous stands with some soft-wood deciduous trees ($n = 15$). The differences are not statistically significant, probably because the samples are too small. The total sample size from the Bialowieża National Park is much larger (403), but in earlier years the construction of nests was evaluated only by inspecting them from the outside, without crushing the nest walls. Hence it was impossible to distinguish between types 1 and 2. All these data nevertheless strongly support the conclusion that not a single nest in the sample represented type 3.

It should be stressed that the Bialowieża sample comes exclusively from primeval forest, while the other samples are of mixed character, containing various proportions of nests from habitats transformed by man. There is a strong indication that wood pulp is largely used in extensive natural or semi-natural forests, while in other habitats other materials may appear. For example, in data from the Polish nest-record scheme wood-pulp nests constituted 92.5% of the forest sample ($n = 1140$), but only 87.4% of the sample from rural and suburban woodlands ($n = 206$). Moreover, among the nests without wood pulp ($n = 64$), including 12 nests without any plastering, the majority (83%) were from the

southern half of Poland, and only 11 (17%) from the northern half. Another sample from southern Poland (Bocheński 1968, and *in litt.*), composed of nests collected in semi-natural forests and in suburban woodland in Cracow, also supports the suggestion that anthropogenic habitats contain more nests of type 3: whereas among his nests from natural habitats type 3 was represented by only 1% ($n=95$), in a sample of 16 nests from Cracow suburban woodland such nests constituted 30%. This makes one suspect that the Czechoslovakian data largely originate from habitats transformed by man, and indeed this is the case; 72% of them are from transformed or anthropogenic habitats (Pikula 1970).

Discussion

Before evaluating these differences in the use of nest materials one should try to answer the question, to what extent the local climate may influence a Song Thrush's ability to construct a proper nest. It is well known that birds, including Song Thrushes, usually build their nests during the early morning hours (e.g. Siivonen 1939, our own observations), though this period of the day must also accommodate other competing activities such as territorial defence, singing and foraging. One may suspect that the higher humidity in the early morning is the main reason. As regards the Song Thrush, detailed observations of captive pairs (Siivonen 1939, Stahl 1987) have shown that the female before plastering her nest regularly soaks the material (wood pulp, in the cases observed) in water. All nests found during the construction phase either in Finland or in Poland were very wet, obviously too wet to have been softened by saliva alone (as suggested in some handbooks). Therefore one may suspect that the absence of water or morning dew in places with a dry climate may be a serious hindrance for breeding Song Thrushes. The Blackbird seems to be less dependent on the humidity of the local climate for two reasons: the ability to build some nests almost devoid of a mud-layer, and the preference for locating nests on a more solid foundation (Bocheński 1968, Tomialojć, *in prep.*). Song Thrush nests, which are often poorly supported, sometimes almost hanging in the branches, in order to be solid enough to stand up to such situations must be plastered with soaked material, either wood pulp, mud, earth or dung. In some habitats this condition obviously cannot be fulfilled.

The pattern of nest-lining distribution in Europe shows some conformity with the advance of colonization of urban areas by the Song Thrush. It is generally acknowledged that the western European and some southern European populations of this species give evidence of much older and more advanced adaptation to urban and suburban conditions than the northern and eastern populations (Cramp 1988, Glutz & Bauer 1988). The British population in particular has been thriving for almost 100 years in the man-made environment which has been in the process of formation since late Neolithic times (Simms 1971, Kirby 1987). Very intensive forest management, involving the practice of coppice-with-standards, for centuries kept British woodlands poor in rotten wood; and this material was probably even scarcer in farmland. This may have forced the British population to turn to substitutes such as

earth or dung, potential materials which are usually wet under British climatic conditions.

It is interesting to note that the Song Thrushes introduced in the southern hemisphere from Britain, and almost certainly taken from anthropogenic habitats, 'brought with them' the secondary habit of using mud, clay or dung for nest plastering. This is especially clear in Australia, where in the rather dry climate of the Melbourne area no wood pulp, only earth is used (Pizzey 1980). In New Zealand, with a more humid, oceanic climate and many introduced European trees, the use of mud seems to predominate locally (Falla *et al.* 1967) but wood pulp, with some earth occasionally included, is said to be the usual material (Oliver 1955). This suggests that what was, presumably, an enforced 'preference' was largely reversed when conditions were again suitable for reversion to the original habit.

In continental Europe the colonization of urban habitats by Song Thrushes has been more recent, probably in part because of the lesser extent of green spaces and the drier local climate of cities, chiefly central European ones. Nevertheless, the species began to be reported from urban habitats during the late 19th century, originally mainly from German territories (Schuster 1904, Glutz & Bauer 1988). By 1960 this colonization had spread eastwards to reach cities of western Poland such as Szczecin and Wrocław and, less certainly, Gdańsk (Dyrcz 1963, Graczyk 1963). More recently, however, there has been a retreat from Polish and some German and British cities (Simms 1971, Tomialojć & Profus 1977, Bezzel 1982, Anon. 1984, Luniak 1990, Tomialojć 1990), which has been tentatively attributed to the increasing human impact on the urban environment, especially the elimination of the bush and ground-litter layer in parks. Eichler (1986) suggested that shortage or deterioration of the quality of available food, due to chemical pollution, might be the reason, though he was aware of the fact that the Blackbird in spite of its similar diet was continuing to increase in the same cities. Both reasons seem improbable in view of the well known ability of Song Thrushes to nest high in trees and to forage in open areas, as well as the fact that Blackbirds continue to prosper. Hence, problems with nest construction might be the main cause.

In this connection a contrast between the situation in Poland and Czechoslovakia seems to be especially intriguing. It appears that while in several Czechoslovakian cities Song Thrushes are quite numerous breeding birds, e.g. reaching densities of 53 pairs per 10 ha in Prague parks (Bialek *et al.* 1980, Stastny *et al.* 1987), or of 8.4–11.7 pairs per 10 ha in Ostrava (Pavelka 1988), in urban parks in the Polish cities of Legnica and Wrocław, not very distant and almost identical structurally with those in Ostrava, Song Thrush densities are below 2 pairs per 10 ha and are decreasing constantly to the point of local extinction (Tomialojć 1970, Tomialojć & Profus 1977, R. Cisakowski, in prep.). It seems that food resources cannot be responsible, as Polish urban parks are known to abound with earthworms and other invertebrates (Dyrcz 1969), and Blackbird populations are dense, though less dense than in Czechoslovakia. Hence two other possibilities may be invoked: difficulties in nest construction, or differential predation pressure. I have no

quantitative data adequate for testing the second possibility so far, though there are some indications that the numbers or efficiency of corvid and mustelid nest-predators may be higher in Polish than in Czechoslovakian cities.

There is still one difference between most Polish and Czechoslovakian territories: in the annual level of precipitation. In Polish lowlands it is mostly 450–650 mm only, while in Polish mountains and in Czechoslovakia it is 650–1200 mm per year (Steinhauser 1970). Higher precipitation may influence positively both the food resources and the ability to use earth for nest plastering.

From what has been said it will be apparent that Song Thrushes in urban areas, as also in farmland and intensively managed woodland, may have difficulty in collecting suitable material for lining their nests. Some populations, chiefly those living in more humid climate, have 'solved' this problem by using secondary types of material (earth or dung), others have not done so, while still others, in primeval or natural forests, have not been forced to change their original habit. It may be that northeastern Polish, Russian and Scandinavian populations are unable to colonize cities because they are too conservative in their use of nest-lining materials, and not necessarily because they are unable to overcome the barrier created by their shyness.

It would be of interest to make a comparative study of the use of nest-lining materials by Song Thrushes in different habitats in Britain, concentrating on populations in urban areas, farmland, and the last-remaining extensive forests such as the New Forest or old oak woodland. The results could falsify the interpretation offered above.

Under present conditions of wholesale deforestation and dry climate, it seems certain that Song Thrushes attempting to nest in Mediterranean lowland habitats would face similar problems to those in central European cities and parks. If my explanation is correct, then the Italian Song Thrushes nesting at lower montane elevations should show a clear preference for stream- or river-valley habitats, and should avoid dry south-facing slopes. It is intriguing also why this species avoids nesting in the anthropogenic landscape not only of Italy, but also of the northern slopes of the Alps in Switzerland (Glutz & Bauer 1988). There may of course be some other constraints, which would need careful evaluation.

More generally, it may be suggested that limitations imposed by the need for special nest materials should be investigated in other species where the reasons for limits of range or breeding habitat are not immediately obvious. Under urban conditions of central European cities it may be impossible for species such as the Chaffinch *Fringilla coelebs* or Long-tailed Tit *Aegithalos caudatus* to find enough mosses or lichens to construct or camouflage their nests. It is well known that both groups of plants tend to disappear from badly polluted urban and suburban habitats, so that it can hardly be coincidence that birds that make extensive use of mosses and lichens in their nests show a clear decline in big cities (Tomialojć & Profus 1977, Luniak 1990), while still prospering in natural forests (Tomialojć *et al.* 1984, Tomialojć 1990).

In the Mediterranean region, there are a number of species which do not breed although they are very common in the rest of Europe. One

group consists of species that prefer fairly humid habitats even in more northerly areas: *Prunella modularis*, *Acrocephalus palustris*, *Sylvia borin*, *Phylloscopus sibilatrix*, *P. trochilus*, *Regulus regulus*. The first and last of these use a lot of moss, usually wet, for building their bulky nests. The others build their nests of dry fragments of vegetation (leaves, grasses, twigs), which under central European conditions tend to be flexible and soft if collected in the early morning when humidity is high. Perhaps even more surprising is the avoidance of Mediterranean lowland habitats by species tolerant of relatively dry places such as, in addition to the Song Thrush, *Phylloscopus collybita*, *Anthus trivialis* and *Emberiza citrinella*.

I suspect that most of these species do not breed in southern European lowlands not necessarily because of high temperature, food shortage etc., but because they face unknown problems of nest construction or nest concealment, or because they would suffer too high nest mortality from a diverse array of mammalian, ground or climbing predators. To falsify this hypothesis, comparative studies of nest construction and breeding biology of central European and Mediterranean, conspecific or congeneric populations would be necessary.

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Weights of some birds from Fiji

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As there is a paucity of recorded body weights for birds from the South Pacific in both the literature and in museum data those recorded from mist-netting operations in Fiji are presented here along with some obtained from the National Museum of New Zealand. As workers begin to investigate topics such as flight, ecological variations, taxonomy, energetics and growth rates, the need for weights of free-living birds from the low latitudes of the South Pacific will increase.

The bulk of these data were recorded on Ohaus triple beam balances between January 1974 and December 1976. The remainder were measured on Pesola spring balances. All birds were free flying adults unless otherwise stated. The island of origin and, where known, the sex of the bird are shown and apply to succeeding data until changed. The major netting sites on Viti Levu were the mountain forests of Nadarivatu and the Tailevu lowlands.